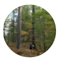
# Wildlife implications across snag treatment types in jack pine stands of Upper Michigan

**Article** *in* Forest Ecology and Management · February 2018

DOI: 10.1016/j.foreco.2017.10.013

Shelby A Weiss
The Ohio State University



Greg Corace
U.S. Fish and Wildlife Service

Eric Toman
The Ohio State University

Charles Goebel
University of Idaho

Forest Ecology and Management 409 (2018) 407–416

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

# Wildlife implications across snag treatment types in jack pine stands of Upper Michigan

Shelby A. Weiss[a,*], R. Gregory Corace III[b], Eric L. Toman[a], Daniel A. Herms[c,1], P. Charles Goebel[a,2]

[a] School of Environment and Natural Resources, The Ohio State University, 2021 Coffey Road, Columbus, OH 43210, USA
[b] U.S. Fish and Wildlife Service, Seney National Wildlife Refuge, 1674 Refuge Entrance Road, Seney, MI 49883, USA
[c] Department of Entomology, The Ohio State University, 1680 Madison Avenue, Wooster, OH 44691, USA

## ARTICLE INFO

*Keywords:*
Ecological forestry
Jack pine
Snags
Fire
Woodpeckers
Subcortical insects

## ABSTRACT

Standing dead trees, or snags, represent post-disturbance biological legacies in forest ecosystems, and intentional creation of new snags is increasingly common during forest treatments. The abundance, volume, size, and distribution of snags can affect wildlife communities and stand-level biological diversity. Characteristics such as the wood properties of different tree species, environmental conditions, and cause of tree death (e.g., insects, disease, senescence, wind, fire) can influence decomposition and subsequent use of snags by wildlife. The objectives of this study were to characterize decay patterns in jack pine (*Pinus banksiana*) snags that had been killed by prescribed fire, topping, and girdling and determine the effects of these treatments on subsequent snag use by subcortical insects and primary cavity-nesting birds. The prescribed fire, topping, and girdling treatments were implemented in 2003, 2004, and 2007, respectively; bird excavations were quantified in 2014 and insect activity was measured in 2016. One-way analysis of variance tests were used to examine any differences among treatments in snag characteristics, decay characteristics, past insect activity, and past use by birds. An information theoretic approach to model selection was then used to rank potential predictors of bird foraging activity and cavities. The topping treatment had unique decay characteristics relative to the other two treatments; topped snags had the highest levels of past insect colonization, were softer, and had higher proportions of loose bark remaining on the boles. Trees killed by prescribed fire had the greatest number of foraging excavations and cavities. Girdled snags had the lowest evidence of past insect colonization and showed different levels of decay and insect use at different vertical positions on the snag bole. Comparison of candidate models showed that a model containing treatment type alone was the highest ranked when predicting foraging by birds, while snag diameter was the highest ranked when predicting the presence of cavities. A model containing treatment and snag density was also a highly ranked for predicting cavity presence. Our findings suggest that different jack pine snag treatments result in unique decay trajectories that may influence snag use by an array of wildlife taxa. Our characterization of three snag creation treatments can also inform options for generating snags, depending on the desired outcome, when management for biological legacies and wildlife habitat is of interest within mixed-pine forests of the Great Lakes region.

## 1. Introduction

Dying trees, standing dead trees (snags), and downed woody material have numerous ecological functions and contribute to structural complexity and biodiversity within forests (Harmon et al., 1986, Franklin, 1988). For example, dying trees increase availability of resources such as light, nutrients, and water, and provide structure and food for a wide range of taxa (Franklin et al., 1987). A diversity of fungi, plants, and animals utilize snags and downed wood throughout their life cycles (Boddy, 2001, Jonsell and Weslien, 2003, Jonsson et al., 2005, Lonsdale et al., 2008).

Within conifer forests of the Great Lakes and boreal regions farther north, past management activities have, in some instances, homogenized stand structure and composition in ways that decrease

---

[*] Corresponding author.
*E-mail address:* shlbweiss@gmail.com (S.A. Weiss).
[1] Present address: 107 N. Walnut St., Wooster, OH 44691, USA.
[2] Present address: Department of Forest, Rangeland, and Fire Sciences, University of Idaho, 875 Perimeter Drive, Moscow, ID 83844, USA.

http://dx.doi.org/10.1016/j.foreco.2017.10.013
Received 18 July 2017; Received in revised form 4 October 2017; Accepted 7 October 2017
0378-1127/

resilience to catastrophic disturbance (Bergeron et al., 1998, Perry, 1998, Drever et al., 2006). Additionally, widespread fire suppression and land use changes have altered many forests, resulting in reduced complexity and diversity relative to pre-European settlement conditions (Schulte et al., 2007, Tucker et al., 2016). Although forest management aimed at timber production often has been implicated in forest simplification, forest management specifically directed at wildlife habitat may also fail to generate all structural features characteristic of natural disturbance regimes. For example, jack pine (*Pinus banksiana*) stands on public lands in Lower Michigan are managed for the endangered Kirtland's warbler (*Setophaga kirtlandii*). Treatments to establish breeding habitat begin by clear-cutting mature jack pine, followed by artificial regeneration (hand or machine planting) of jack pine seedlings in an opposing wave pattern (MDNR et al., 2015). Seedlings are planted to produce dense patches of regeneration and other areas are left unplanted and open. While these practices have contributed to the recovery of this neotropical migrant songbird, they have also resulted in unnatural patterns of regeneration (Kashian et al., 2017), with significantly lower levels of snags in plantations (3 snags $ha^{-1}$) relative to fire-regenerated stands (252 snags $ha^{-1}$; Spaulding and Rothstein, 2009).

Snags are used by a variety of invertebrates, including subcortical insects that complete a portion of their life cycle beneath the bark of woody plants. Many of these insects colonize certain tree species or utilize trees at specific stages of decay (Byers, 1995, Saint-Germain, 2007). Evidence of past colonization of snags by bark beetles (Curculionidae: Scolytinae) and wood-borers (Cerambycidae: Buprestidae) include entrance and emergence holes on the bole and larval galleries (Wood, 1982). According to Boulanger and Sirois (2007), colonization of dead trees by subcortical insects proceeds in two successional "waves." The first wave occurs when insects colonize standing snags soon after tree death. The second wave occurs with epigeic species that utilize snags after they have fallen. Snag size and stem density are known to influence colonization by subcortical insects as well as subsequent excavation by predatory birds (Saint-Germain et al., 2004, Farris and Zack, 2005). Colonization by insects and foraging by birds are also thought to accelerate snag decay (Harmon et al., 1986, Farris et al., 2004).

A wide range of vertebrates also use snags for shelter, including bats (Chioptera), rodents, bears, and herpetofauna (Holloway and Malcolm, 2007; Bull, 2002; Foster and Kurta, 1999; Johnson and Pelton, 1981). Woodpeckers (Picidae) and even songbirds (e.g., black-capped chickadee, *Poecile atricapillus*) excavate cavities and forage for insects on decaying trees. Primary cavity-nesting bird species often construct cavities that are subsequently exploited by secondary cavity-nesting species (e.g., wood duck, *Aix sponsa*; American kestrel, *Falco sparverius*). However, snags may become less suitable for foraging by birds as snags deteriorate, as colonization by subcortical insects peaks within one to three years following tree death in pine ecosystems (Farris et al., 2002, Farris and Zack, 2005). As decay progresses, more decayed snags are thought to become more suitable for cavity excavation (Farris and Zack, 2005). Previous research suggests that proximate cause of tree death affects the probability of cavity excavation, as does wood softness, snag size, and stem density (Petit et al., 1985, Parks et al., 1999, Lehmkuhl et al., 2003, Bagne et al., 2008).

The concept of ecosystem management calls for greater retention of snags and other biological legacies in managed forests (Franklin et al., 1987, Harmon, 2001, Dudley and Vallauri, 2005). Such management maintains structural complexity and biodiversity (Franklin et al., 2002, Lindenmayer and Noss, 2006). Recognizing the importance of retaining or augmenting the abundance or volume of snags in forests, previous studies have investigated methods for creating snags such as girdling and topping of trees, herbicide application, and/or inoculating trees with fungi (Bull and Partridge, 1986, Chambers et al., 1997, Hallett et al., 2001, Brandeis et al., 2002, Shea et al., 2002, Filip et al., 2004, Arnett et al., 2010). Wildlife responses to snag creation and decay processes have been studied more in the western United States than in the sub-boreal, mixed-pine forests of the Great Lakes region. One study conducted in Upper Michigan investigated snag creation methods and found that jack pine snags generated by girdling developed into advanced decay classes faster than snags created by topping or prescribed fire (Corace et al., 2013). However, wildlife response to the methods of snag creation was not evaluated. Moreover, recent proposals to list the northern long-eared bat (*Myotis septentrionalis*) and other bat species that utilize snags under the *Endangered Species Act* have heightened the need for more research that investigates snag management within an ecological context.

We focus here on two types of snag use by forest birds that we collectively term an excavation: (1) use of a snag for a cavity (be it for cover or nesting) and (2) use of a snag for potential food resources. The objectives of this study were to quantify differences in the treatments implemented and evaluated by Corace et al. (2013) in terms of decay variables and use by subcortical insects and primary cavity-nesting bird species, as well as to explore which variables best predict variation in observed bird excavations. Understanding the interactions between snag decay, insects, birds, and the environment can contribute to a better understanding of the outcomes of forest treatments that aim to retain or enhance biological legacies and provide complexity in mixed-pine forests.

## 2. Material and methods

### 2.1. Study site

Our study was conducted at Seney National Wildlife Refuge (SNWR) in eastern Upper Michigan (N46.288, W85.945). Proximity to the Great Lakes influences the local climate. Most winds are typically from the southwest to the northwest. The area experiences 81 cm of annual precipitation on average, and the average daily humidity ranges from 50 to 60% (USFWS, 2009). Temperatures typically range from −14 to 26 degrees Celsius (MRCC, 2017). The landscape is part of the Seney Sand Lake Plain ecoregion (Albert, 1995). The majority of upland soils are xeric sands that historically supported red pine (*P. resinosa*) forests, with a lesser component of eastern white pine (*P. strobus*). During the late 19th and early 20th centuries, those stands accessible to logging across the wetland matrix were cut and burned outside the natural range of variation (Losey, 2003); stands inaccessible to logging were left alone and now provide benchmarks for studying fire regimes (Drobyshev et al., 2008a, Drobyshev et al., 2008b), forest structure and regeneration dynamics (Corace et al., 2013, Nyamai, 2013, Nyamai et al., 2014), and wildlife communities (Corace et al., 2014). Altered stands are currently dominated by jack pine and have different structure, wildlife communities, and associated fire behavior compared to benchmark stands (red pine). As such, the restoration of ecosystems dominated by red pine and eastern white pine and the restoration of a fire regime with a fire return interval of low to mixed-severity fires approximately every 25–35 years are priorities for management (Drobyshev, 2014).

### 2.2. Creation and selection of snags

All forest stands in which we worked were part of a previous snag study (Corace et al., 2013), itself part of a larger effort to restore red pine, reduce heavy fuels (e.g., jack pine), and prepare sites for prescribed fire. All stands included in this study were growing on the white pine/blueberry (*Vaccinium*)/trailing arbutus (*Epigaea repens*) habitat type of the soil classification of Burger and Kotar (2003). Red pine and eastern white pine are late successional dominants and jack pine is the common dominant at earlier successional stages on this soil type.

In brief, snags were created mechanically in two harvested stands and in an additional stand via a prescribed fire. Harvesting occurred in mixed-pine stands with even-aged jack pine being the most common

**Table 1**
Primary cavity-nesting bird species (listed alphabetically by common name) known to be present at Seney National Wildlife Refuge and their reported cavity dimensions. Relative abundance values were derived from Michigan Breeding Bird Atlas II data (Chartier et al., 2011), research (Corace et al., 2014), and planning documents (USFWS, 2009).
Source: Birds of North America *Online* (Browse Species), unless otherwise noted. For individual species accounts, see https://birdsna.org/Species-Account/bna/species

| | Reported cavity heights from ground (m) | Reported cavity entrance diameters (cm) | Reported cavity depths (cm) | Relative abundance at SNWR[c] |
|---|---|---|---|---|
| Black-capped chickadee (*Poecile atricapillus*) | 0–20 + | 2.8[b] | 10–46 | Abundant |
| Boreal chickadee (*Poecile hudsonicus*) | 0.1–10.5 | 2.4 | 12.7–30.5 | Rare |
| Black-backed woodpecker (*Picoides articus*) | 2.7 – 11 | 3.3–4.4 | 21–41 | Uncommon |
| Downy woodpecker (*Picoides pubescens*) | 4.7–13.5 | 2.5–3.8 | 15.2–30 | Common |
| Hairy woodpecker (*Picoides villosus*) | 1–18.3 | 3.8–5.1 | 20.3–38.1 | Common |
| Northern flicker (*Colaptes auratus*) | 1.3–11.4 | 6.45–8.3 | 14.9 | Common |
| Pileated woodpecker (*Dryocopus pileatus*) | 13.1–35.3 | 8–12 | 47.6–60 | Common |
| Red-headed woodpecker (*Melanerpes erythrocephalus*) | 7–12.4 | 5.6–5.9 | 14.3 | Rare |
| Red-bellied woodpecker (*Melanerpes carolinus*) | 2–15 | 5.1–6.4[a] | 22–32 | Rare |
| Red-breasted nuthatch (*Sitta canadensis*) | 3.5–15.7 | 2.0–9.5 | 2.0–7.0 | Common |
| Three-toed woodpecker (*Picoides dorsalis*) | 5.2–7.7 | 3.8–4.7 | 24.1–30.5 | Rare |
| Yellow-bellied sapsucker (*Sphyrapicus varius*) | 2–9 | 3.2–4.1 | 27 | Common |

[a] Jackson (1976).
[b] Cooper and Bonter (2008).
[c] Chartier et al. (2011), Corace et al. (2014), and USFWS (2009).

overstory species (Corace et al., 2009). Red pine and eastern white pine were favored in these stands and were left as seed trees. Growing season harvesting removed all merchantable jack pine (> 12 cm diameter breast height or DBH). Harvested stands had variable retention of ~10–70% of the pre-treatment basal area and some scarification for red and eastern white pine regeneration (Nyamai, 2013). The patterns resulting from these harvests yielded a heterogeneous distribution of residual as suggested by Lindenmayer and Franklin (2002) for conifer stands being managed for biodiversity. Differences in pre-treatment conditions of stands used in this study were primarily in age and time since last treatment, rather than surficial geology, successional trajectories, or composition and structure.

The prescribed fire occurred in 2003 resulting in a 105-ha burned area with > 70% jack pine mortality and most (~70%) red pine trees alive post-fire. This mixed-severity fire was likely within the range of variation of fires historically found on the landscape (Drobyshev et al., 2008b). The 126-ha topping treatment was implemented in 2004 to reduce fuel loading associated with jack pine, promote regeneration of red pine, and enhance growth of existing red pine and eastern white pine. Relatively large and healthy jack pine trees were cut at ~3 m in height (maximum height logging equipment was able to reach). The girdling treatment took place in 2007 in a timber harvest of approximately 173 ha. Girdling involved using a mechanized processor head to scrape the bark off of the middle sections of trees (generally at a position 1–3 m from the ground). Goals and objectives of the timber harvest were similar to those for the 2004 harvest. For all snags created through mechanical treatments, trees marked for snag creation tended to be larger and healthier and were spaced apart so as to allow equipment to work. On average, snags were spaced 28.6 m ( ± 38.4 m) apart in the topped treatment, 51.7 m ( ± 30.2 m) apart in the girdled treatment, and 8.25 m ( ± 4.0 m) apart in the prescribed fire treatment.

### 2.3. Sampling strategy

Based on the expected needs of primary cavity-nesting birds, Thomas et al. (1979) defined a snag as ≥10.2 cm DBH and ≥1.8 m in height. We applied these criteria when selecting snags to sample. In 2014, 105 snags (35 per treatment) were sampled for excavations (obvious penetrations of the wood from either foraging or cavity development) by birds. In 2016, these same snags were sampled for past subcortical insect activity. Our initial sampling scheme involved resampling a subset of snags from the Corace et al. (2013) study. Sixty-one jack pine snags had been sampled from the girdled treatment and 26 jack pine snags from the topped treatment in that study. For our study herein, we randomly selected 35 girdled jack pines to resample using a random number generator. From the topped snags used in the previous study, we were able to only resample 22 (the other four were not found). Therefore, 13 additional topped jack pine snags were selected to reach 35 total. These additional topped snags were selected by simply walking through the harvested stand and selecting topped snags using bark characteristics to identify jack pines with the size criteria shown above. Snags were not marked within the prescribed fire treatment from the previous study. We therefore sampled snags in this treatment systematically along a transect. From the prescribed fire treatment, we sampled 29 jack pine snags as well as six red pine snags. Red pine snags were included due to the limited number of jack pine snags available for sampling within the treatment area. In 2016, we also sampled 35 live jack pine trees for comparison purposes in a separate jack pine-dominated forest stand at SNWR. These live trees were selected by making stops every 161 m along a road bisecting the stand. At each stop, we sampled three trees along a transect perpendicular to the road at 20 m, 40 m, and 60 m. All live trees were > 10.2 cm in diameter.

### 2.4. Measurements

In June and July of 2014, we measured DBH (cm) and height (m) of all sampled snags. Excavations were identified by noting locations on the bole where deeper notches had been made into the bark or wood. Foraging excavations were distinguished as being more irregularly shaped, having "rougher" edges, and sometimes revealed an insect entrance hole at the center. Cavities were more uniform in shape and had rounded edges (Gorman, 2015). All bird excavations were documented with photographs and the height from the ground of each excavation and associated dimensions (e.g., length, width, and depth) were recorded. Photos and dimensions were reviewed to distinguish between foraging excavations and cavities. Potential cavities were identified based on documented cavity dimensions of primary cavity-nesting species known to occur at SNWR (Table 1). To be considered a potential cavity, the excavation had to be ≥2 cm in diameter, ≥14 cm in depth, and ≥1 m above the ground. Excavations on sections of the snag > 3 m above the ground were identified using binoculars. Visibility was generally unimpeded by fine branches and needles due to the stage of decay of the snags. For cavities higher up on snags, we confirmed potential cavities at a later date by using a ladder to access the excavation. At this time we also confirmed that the internal dimensions met the minimum thresholds above. These methods would likely not have captured any foraging excavations that were very shallow or that failed to penetrate noticeably into the bark or sapwood (e.g., bark flaking).

In June and July of 2016, all snags were relocated using GPS coordinates and their decay characteristics and signs of past colonization by subcortical insects were recorded (described below). Snag decay characteristic metrics were adapted from Angers et al. (2012) and included stem integrity (intact or broken), presence of dead needles, twigs, and/or branches, total bark coverage (e.g., 0–25%, 26–50%, 51–75%, or 76–100%), and wood penetrability ("softness" measured on a four-point scale). The wood penetrability ratings were based on how easily and how far into the bole a 2.5 cm-wide knife blade would penetrate. This value ranged from one (the blade could not penetrate the bole) to four (the blade could easily penetrate the bole). This measurement was taken at breast height in the four cardinal directions. To standardize measurements, the same knife was used on each occasion and the same observer measured penetrability for each sample. The numbers of nearby snags and live trees (> 10.2 cm DBH within a 0.01 ha circular plot) surrounding each snag were also counted.

Insect entrance/emergence holes and galleries and bark looseness were evaluated at three different heights: 0 m, 1.5 m, and 3 m. Although the vast majority of snags were > 3 m in height, not all snags were and in these cases only applicable heights were measured. At each height, bark was removed from a 0.2 m-long band all around the bole (Fig. 1). Bark that could be removed by hand with minimal effort was considered "loose." The number of insect entrance/emergence holes and coverage by galleries were recorded within each band using methods modified from Flower et al. (2013): a gridded, transparent sheet was placed over the area where bark was removed and the number of 1-cm$^2$ grid cells containing a gallery was recorded. The same variables were measured on live trees, with the exception that bark was not removed from the trees and gallery cover was not measured.

### 2.5. Data analyses

To identify differences in levels of insect and bird use and snag characteristics among treatments, variables were compared using one-way analysis of variance tests (ANOVA). These tests were then followed by post-hoc Tukey comparison tests to detect specific differences in variables among treatments. We compared numbers of excavations (e.g., foraging activity and cavities) recorded per snag in each treatment, decay characteristics, snag DBH, stem density (snags and live trees), as well as bark cover and insect use at three heights from the ground. These comparisons were done using R packages "stats" and "multcomp" (R Core Team, 2013; Torsten et al., 2008).

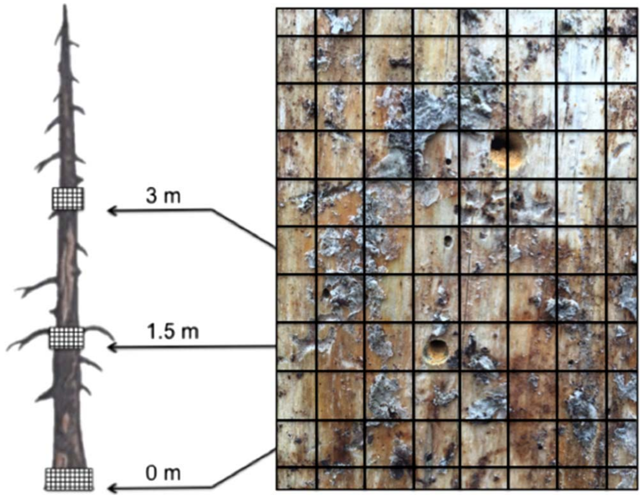


**Fig. 1.** Sampling design for measuring past subcortical insect activity and bark looseness. Twenty-cm sections (vertically) were sampled at three heights (i.e., 0 m, 1.5 m, and 3 m) on each snag/tree. A transparency grid was used to assess gallery cover.

We used Akaike's Information Criteria (AIC; Burnham and Anderson, 2002) to rank candidate models containing combinations of snag, insect, and/or decay variables as predictors of the number of foraging excavations and the presence of cavities. AIC is based on Kullback-Leibler distance and estimates the relative distance of a fitted model from the true (unknown) underlying mechanism(s) responsible for generating what is observed. The model with the lowest AIC is best supported by the data. We used R packages "stats" and "MASS" to run models (R Core Team, 2013, Venables and Ripley, 2002).

We modeled foraging excavations and presence of cavities separately using two sets of candidate models representing multiple potential combinations of variables thought to influence the use of snags by birds and supported by findings from previous studies. As many of the predictors were inter-correlated, we did not develop one global model with all proposed predictors. Snag height was not included in any models because height was predetermined by treatment (e.g., all topped snags were ~3 m in height). Time since treatment was also not used as a predictor variable because each of the three treatments took place in a different year, meaning that treatment effects would be indistinguishable from time effects for a given year.

To construct models of foraging excavation abundance, we used variables related to treatment, snag DBH, stem density, insect activity (all primary cavity-excavators present at SNWR are known to feed on subcortical insects), and combinations of these variables based on previous research related to influences of snag use by birds (Farris et al., 2002, Saint-Germain et al., 2004, Farris and Zack, 2005). We included models representing each of these hypothesized causal variables separately, as well as combined models containing snag DBH, stem density, and insect activity as predictors. Decay variables were not used as predictors in models of foraging excavation abundance because insect and bird foraging activity often peaks 1–3 years after treatments in pine-dominated ecosystems (Farris et al., 2002, Farris and Zack, 2005), whereas our decay variables were measured 9–13 years following treatment. Foraging excavations were treated as count data and modeled using a negative binomial distribution because data were over-dispersed (variance > mean). Negative binomial distributions are useful in modeling over-dispersed count data and include a dispersion parameter (Bliss and Fisher, 1953).

A similar method was used to construct models of cavity presence. Considering previous research findings (Petit et al., 1985, Parks et al., 1999, Lehmkuhl et al., 2003, Bagne et al., 2008), candidate models included variables representing treatment, snag DBH, stem density, decay, and combinations of these. Logistic regression was used to investigate the presence of cavities.

## 3. Results

### 3.1. Comparing treatments

Notable variability in decay characteristics (Table 2), as well as in insect activity and bird use (Table 3) was observed among treatments. In particular, there was a significant difference in the level of bird foraging evidence among treatments ($F_{2,101} = 6.78$, $p < 0.01$). The prescribed fire treatment yielded snags with significantly more foraging excavations per snag than the other two treatments ($p_{F\text{-}G} < 0.01$, $p_{F\text{-}T} = 0.02$). No significant difference in foraging activity was found between the girdled and topped treatments ($p = 0.66$). Although the prescribed fire treatment contained the greatest number of cavities overall, there was no significant difference in cavity presence per snag among the three treatments ($F_{2,101} = 0.824$, $p = 0.44$).

There was also significant variation among treatments in the abundance of insect holes ($F_{2,101} = 19.8$, $p < 0.01$) and galleries ($F_{2,101} = 3.11$, $p = 0.05$). The topped treatment had significantly more insect holes than each of the other treatments ($p < 0.01$ for both). The topped treatment also had more insect galleries than the girdled

**Table 2**
Snag characteristics 9–13 years post-treatment for three different methods of creating snags (i.e., girdling, topping, and prescribed fire) and for live trees sampled for comparison. Diameter at breast height (DBH), stem height (m), integrity (whether the snag is intact), percentage of bark cover (estimated percentage of bark covering a snag), penetrability (a measure of wood hardness based on how easily the sapwood can be punctured), the number of trees per ha, and number of snags per ha for each treatment are listed.

| | DBH (cm) | Height (m) | Integrity | | % Bark Cover | Penetrability (1 – 4)[a] | Trees ($ha^{-1}$) | Snags ($ha^{-1}$) |
|---|---|---|---|---|---|---|---|---|
| | Mean *(SD)* | Mean *(SD)* | Intact | Broken | Mean *(SD)* | Mean *(SD)* | Mean *(SD)* | Mean *(SD)* |
| Girdled | 30.2 *(5.6)* | 7.4 *(3.9)* | 7 | 28 | 48 *(24)* | 1.7 *(0.4)* | 183 *(1 4 4)* | 31 *(53)* |
| Topped | 33 *(3.6)* | 3.4 *(0.3)* | 0 | 35 | 53 *(27)* | 2.2 *(0.5)* | 180 *(1 9 7)* | 26 *(56)* |
| Prescribed Fire | 27.7 *(8.4)* | 5.6 *(3.0)* | 7 | 27 | 40 *(29)* | 1.8 *(0.4)* | 82 *(1 5 1)* | 200 *(1 6 0)* |
| Live | 20 *(5.4)* | 8.9 *(1.3)* | 35 | 0 | 99 *(3)* | 2.0 *(0.1)* | 386 *(2 6 0)* | 37 *(65)* |

[a] Four-point scale with 1 being the least penetrable and 4 being the most penetrable.

treatment ($p = 0.04$), although there were no significant difference between topped and prescribed fire treatments ($p = 0.47$). There were also no significant differences between insect hole abundance or gallery cover between the girdled and prescribed fire treatments ($p_{\text{holes}} = 0.82$, $p_{\text{galleries}} = 0.40$).

Insect holes and foraging excavations in all treatments were concentrated at lower heights on snags (Fig. 2A). When comparing levels of insect activity among treatments at each height along the bole, there were significant differences among treatments in the abundance of insect holes present at each height: 0 m: $F_{2,101} = 28.1$, $p < 0.01$; 1.5 m: $F_{2,100} = 59.03$, $p < 0.01$; 3 m: $F_{2,82} = 5.18$, $p = 0.01$. However, only at the middle height (1.5 m) were there significant differences for galleries ($F_{2,99} = 14.72$, $p < 0.01$). Topped snags had more insect holes than both girdled and prescribed fire snags at the bottom and middle heights ($p < 0.01$ in all four comparisons), and more insect holes than girdled snags at 3 m ($p = 0.01$). At the 1.5-m section, girdled snags had significantly fewer galleries than the other two treatments ($p < 0.01$ in both). Live trees had very little evidence of past bird excavations or insect activity. No cavities were observed on live trees, only one live tree had evidence of foraging activity, and only five of the 35 (14%) had insect entrance or exit holes within the sections sampled (galleries were not measured).

There was a significant difference in penetrability of snags among treatments ($F_{2,101} = 16.89$, $p < 0.01$). Topped snags had greater levels of penetrability than the prescribed fire and girdled snags ($p < 0.01$ for both). Bark retention on snags did not differ significantly among treatments ($F_{2,101} = 2.07$, $p = 0.13$), although average bark looseness did ($F_{2,101} = 12.32$, $p < 0.01$). Topped snags had a greater percentage of loose bark on average than either the girdled ($p = 0.03$) or prescribed fire snags ($p < 0.01$). Prescribed fire snags also had significantly less loose bark present than girdled snags ($p = 0.04$). In examining how bark retention compared among treatments by vertical height, differences were observed among treatments at all three heights (0 m: $F_{2,101} = 5.20$, $p = 0.01$; 1.5 m: $F_{2,100} = 12.1$, $p < 0.01$; 3 m: $F_{2,82} = 11.23$, $p = 0.01$; Fig. 2). The girdled and prescribed fire snags

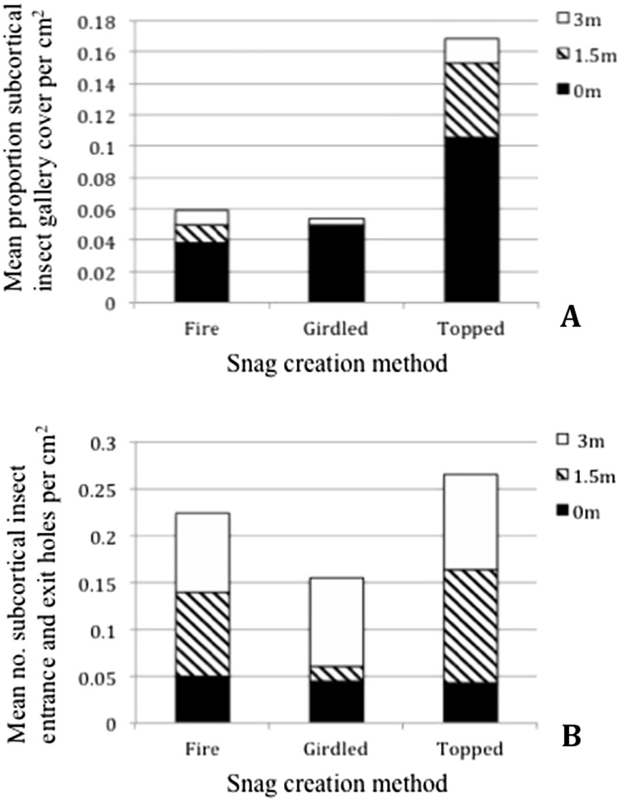


**Fig. 2.** (A) Average subcortical insect gallery cover per $cm^2$ on snags within sections sampled at three heights (i.e., 0 m, 1.5 m, 3 m) on snags created by prescribed fire, girdling, and topping. (B) Average subcortical insect entrance and exit holes per $cm^2$ within sections sampled at three heights (i.e., 0 m, 1.5 m, 3 m) on snags created by prescribed fire, girdling, and topping.

**Table 3**
Evidence of past activity by birds and subcortical insects 9–13 years post-treatment for three different methods of creating snags (i.e., girdling, topping, and prescribed fire) and for live trees sampled for comparison. Total number of foraging excavations, mean (standard deviation) number of foraging excavations per snag, total number of cavities, the average number of insect entrance and exit holes per cm squared, the number of insect entrance and exit holes per cm squared broken out by size, and average "coverage" by insect galleries beneath the bark of snags (number of 1-$cm^2$ cell intersecting a gallery on a gridded transparent sheet) are listed.

| | Foraging excavations | | Cavities | Entrance and exit holes ($cm^{-2}$) | Entrance and exit holes ($cm^{-2}$) by size | | | Gallery cover ($cm^{-2}$) |
|---|---|---|---|---|---|---|---|---|
| | Total | Mean (SD) | Total | Mean *(SD)* | # Small < 0.2 mm Mean *(SD)* | # Medium 0.2–0.5 mm Mean *(SD)* | # Large > 0.5 mm Mean *(SD)* | Mean *(SD)* |
| Girdled | 152 | 4.3 *(8.0)* | 2 | 0.02 *(0.03)* | 0.01 *(0.01)* | 0.01 *(0.01)* | < 0.01 *(< 0.01)* | 0.05 *(0.04)* |
| Topped | 252 | 7.2 *(11.1)* | 3 | 0.08 *(0.06)* | 0.05 *(0.03)* | 0.02 *(0.01)* | 0.01 *(< 0.00)* | 0.09 *(0.05)* |
| Prescribed Fire | 546 | 16.1 *(19.7)* | 11[a] | 0.03 *(0.02)* | 0.01 *(0.01)* | 0.01 *(0.01)* | < 0.01 *(< 0.01)* | 0.07 *(0.08)* |
| Live | 23 | 0.7 *(3.9)* | 0 | < 0.01 *(< 0.01)* | < 0.01 *(< 0.01)* | < 0.01 *(< 0.01)* | < 0.01 *(< 0.01)* | NA (NA) |

[a] Cavities were found in 5 snags, two of which were red pines.

differed significantly at all heights measured ($p < 0.01$ in all three cases). The girdled snags had greater bark coverage at 0 m and 3 m relative to the prescribed fire snags ($p < 0.01$ for both), but less coverage at 1.5 m ($p < 0.01$). The girdled treatment also differed in bark coverage from the topped treatment at the 1.5-m and 3-m sections, having greater coverage at 3 m ($p < 0.01$), but having significantly less bark remaining at 1.5 m ($p < 0.01$).

Differences in stem density of nearby snags and nearby live trees were observed among treatments ($F_{2,101} = 32.61$, $p < 0.01$ for snags; $F_{2,101} = 4.09$, $p = 0.02$ for live trees). Snags were aggregated more densely in the prescribed fire treatment than in the other treatments ($p < 0.01$ for both), and had fewer nearby live trees than the other treatments ($p = 0.04$ for both). No significant differences in snag or tree densities were observed between the girdled and topped treatments ($p_{snags} = 0.97$, $p_{trees} = 0.99$). Differences also existed among treatments in average diameter ($F_{2,101} = 6.93$, $p < 0.01$) and height ($F_{2,101} = 17.07$, $p < 0.01$) of the snags. Snags in the prescribed fire treatment were significantly smaller in diameter than snags in the topped treatment ($p < 0.01$), although no other significant differences in diameter were noted ($p_{G\text{-}T} = 0.11$, $p_{G\text{-}F} = 0.21$). Topped snags were on average shorter than both the prescribed fire ($p = 0.01$) and girdled ($p < 0.01$) snags. The girdled snags were on average taller than the snags from the prescribed fire treatment ($p = 0.03$).

### *3.2. Generalized linear models*

Among the candidate models predicting frequency of bird foraging activity, the model containing only an effect of snag creation method ("treatment") was the best supported (Table 4). The prescribed fire treatment was a significant predictor of the abundance of foraging excavations (Table 6), with nearly twice as much foraging activity predicted for a snag in the prescribed fire treatment compared to the girdling treatment (or 1.89 times; on average 2.78 ± 0.34; Table 6). And 1.4 times as much foraging activity was predicted in the prescribed fire treatment compared to the topped treatment. The next highest ranked model for foraging excavations contained treatment and insect holes as explanatory variables. However, insect holes as a predictor did not have a significant effect on the abundance of foraging excavations in the model (Table 6).

In comparing candidate models that predicted cavity presence, the model containing only snag DBH had the greatest support (Table 5). The odds of a cavity being present was 1.14 times more likely for every centimeter increase in diameter. The next highest ranked model for presence of cavities contained treatment variables and number of nearby snags as predictors, and both had significant effects on cavity presence. The odds of a cavity being present were found to be 9.09 times more likely within the prescribed fire treatment relative to the other two treatments. However, cavities were nearly a third less likely to be present for every increase in the number of nearby snags in the prescribed fire treatment (Table 6).

**Table 4**
Comparison and ranking of candidate generalized linear models predicting the number of foraging excavations in snags among three snag creation treatments: girdling, topping, and prescribed fire. Models used a negative binomial distribution. Model predictors, number of parameters (K), Akaike's Information Criterion (corrected for smaller sample sizes), $AIC_C$ rescaled from the lowest score ($\Delta\ AIC_C$), and Akaike weights ($w.AIC_C$) for each model are listed. The top two models are identified in bold.

| Predictor type | Predictors | K | AICc | ΔAICc | w.AICc |
|---|---|---|---|---|---|
| **Treatment** | **Trtmt** | **4** | **645.56** | **0.00** | **0.27** |
| Snag diameter | DBH | 3 | 654.89 | 9.33 | 0.00 |
| Stem Density | NearSnags | 3 | 652.01 | 6.45 | 0.01 |
| | NearTrees | 3 | 657.91 | 12.36 | 0.00 |
| | NearSnags + NearTrees | 4 | 654.25 | 8.69 | 0.00 |
| Insect activity | Holes | 3 | 654.94 | 9.39 | 0.00 |
| | Galleries | 3 | 657.37 | 11.82 | 0.00 |
| Combinations | DBH + Holes | 4 | 654.72 | 9.17 | 0.00 |
| | DBH + Galleries | 4 | 656.31 | 10.75 | 0.00 |
| | **Trtmt + Holes** | **5** | **646.20** | **0.64** | **0.20** |
| | Trtmt + Galleries | 5 | 647.63 | 2.08 | 0.10 |
| | Trtmt + DBH | 5 | 647.97 | 2.41 | 0.08 |
| | Trtmt + NearSnags | 5 | 648.02 | 2.47 | 0.08 |
| | Trtmt + NearTrees | 5 | 647.15 | 1.59 | 0.12 |
| | Trtmt + DBH + Holes | 6 | 648.64 | 3.08 | 0.06 |
| | Trtmt + DBH + Galleries | 6 | 650.07 | 4.52 | 0.03 |
| | Trtmt + NearSnags + NearTrees | 6 | 649.73 | 4.18 | 0.03 |

**Table 5**
Comparison and ranking of candidate generalized linear models predicting the presence of cavities among three snag creation treatments: girdling, topping, and prescribed fire. Models used a binomial distribution. Model predictors, number of parameters (K), Akaike's Information Criterion (corrected for smaller sample sizes), $AIC_C$ rescaled from the lowest score ($\Delta\ AIC_C$), and Akaike weights ($w.AIC_C$) for each model are listed. The top two models are identified in bold.

| Predictor type | Predictors | K | AICc | ΔAICc | w.AICc |
|---|---|---|---|---|---|
| Treatment | Trtmt | 3 | 70.72 | 5.52 | 0.01 |
| **Snag diameter** | **DBH** | **2** | **65.21** | **0.00** | **0.15** |
| Stem density | NearSnags | 2 | 67.36 | 2.15 | 0.05 |
| | NearTrees | 2 | 70.05 | 4.85 | 0.01 |
| | NearSnags + NearTrees | 3 | 69.59 | 4.38 | 0.02 |
| Decay | Integrity | 2 | 69.98 | 4.77 | 0.01 |
| | Penet | 2 | 70.08 | 4.87 | 0.01 |
| | BarkCover | 2 | 70.09 | 4.88 | 0.01 |
| Combinations | DBH + BarkCover | 3 | 67.20 | 2.00 | 0.06 |
| | DBH + Penet | 3 | 67.46 | 2.26 | 0.05 |
| | DBH + Integrity | 3 | 66.79 | 1.58 | 0.07 |
| | NearSnags + Integrity | 3 | 69.62 | 4.41 | 0.02 |
| | NearSnags + Penet | 3 | 69.53 | 4.33 | 0.02 |
| | NearTrees + Integrity | 3 | 72.19 | 6.99 | 0.00 |
| | NearTrees + Penet | 3 | 72.30 | 7.09 | 0.00 |
| | NearSnags + NearTrees + Integrity | 4 | 71.94 | 6.74 | 0.01 |
| | NearSnags + NearTrees + Penet | 4 | 71.86 | 6.65 | 0.01 |
| | Trtmt + DBH | 4 | 67.35 | 2.14 | 0.05 |
| | **Trtmt + NearSnags** | **4** | **65.45** | **0.24** | **0.13** |
| | Trtmt + NearTrees | 4 | 72.77 | 7.57 | 0.00 |
| | Trtmt + NearSnags + NearTrees | 5 | 66.44 | 1.23 | 0.08 |
| | Trtmt + Integrity | 4 | 72.89 | 7.69 | 0.00 |
| | Trtmt + Penet | 4 | 73.05 | 7.85 | 0.00 |
| | Trtmt + BarkCover | 4 | 73.01 | 7.81 | 0.00 |
| | Trtmt + DBH + BarkCover | 5 | 68.55 | 3.34 | 0.03 |
| | Trtmt + DBH + Penet | 5 | 69.82 | 4.61 | 0.02 |
| | Trtmt + DBH + Integrity | 5 | 68.25 | 3.05 | 0.03 |
| | Trtmt + NearSnags + Integrity | 5 | 67.72 | 2.52 | 0.04 |
| | Trtmt + NearSnags + Penet | 5 | 67.92 | 2.71 | 0.04 |
| | Trtmt + NearTrees + Integrity | 5 | 75.05 | 9.85 | 0.00 |
| | Trtmt + NearTrees + Penet | 5 | 75.21 | 10.00 | 0.00 |
| | Trtmt + NearSnags + NearTrees + Integrity | 6 | 68.60 | 3.39 | 0.03 |
| | Trtmt + NearSnags + NearTrees + Penet | 6 | 69.02 | 3.82 | 0.02 |

## 4. Discussion

The objective of this study was to quantify the effects of different methods to create snags within the context of wildlife utilization. More specifically, we examined the development of overall decay patterns and the response of subcortical insects and primary cavity-nesters 9–13 years after snag treatment. Our approach in identifying and teasing apart differences among treatments was composed of two steps: we first examined how treatments differed on the variables measured and we then asked which variables were best at explaining the variation observed in excavations by primary cavity-nesters across all treatments.

It is important to note the effects the individual treatments had on stand structure. Mechanical treatments (both girdling and topping) resulted in snags that were distributed more evenly throughout the stand compared to the prescribed fire treatment. The prescribed fire treatment produced a denser aggregation of smaller jack pine snags relative to the other treatments. We consider the differences in snag

**Table 6**
Results of the two highest ranked generalized linear models for predicting the number of foraging excavations on snags (modeled using a negative binomial distribution) and for predicting the presence of cavities on snags (modeled using a binomial distribution) across three snag creation treatments (i.e., girdling, prescribed fire, and topping).

| | | Estimate | Odds Ratio | SE | z-value | p-value |
|---|---|---|---|---|---|---|
| *Predicting the number of foraging excavations* | | | | | | |
| Model 1: | Intercept | 1.47 | NA | 0.24 | 6.11 | < 0.01 |
| | Fire | 1.31 | NA | 0.34 | 3.90 | < 0.01 |
| | Topped | 0.51 | NA | 0.34 | 1.51 | 0.13 |
| Model 2: | Intercept | 1.58 | NA | 0.25 | 6.38 | < 0.01 |
| | Fire | 1.30 | NA | 0.33 | 3.90 | < 0.01 |
| | Topped | 0.73 | NA | 0.38 | 1.90 | 0.06 |
| | Holes | −4.69 | NA | 3.33 | −1.41 | 0.16 |
| *Predicting the presence of cavities* | | | | | | |
| Model 1: | Intercept | −6.35 | 0.00 | 2.15 | −2.95 | < 0.01 |
| | DBH | 0.13 | 1.14 | 0.06 | 2.04 | 0.04 |
| Model 2: | Intercept | −2.57 | 0.08 | 0.73 | −3.50 | < 0.01 |
| | Fire | 2.21 | 9.09 | 0.96 | 2.30 | 0.02 |
| | Topped | 0.37 | 1.45 | 0.95 | 0.39 | 0.69 |
| | NearSnags | −1.15 | 0.32 | 0.55 | −2.10 | 0.03 |

stem density to be outcomes of these treatments. Girdling or topping trees with logging equipment necessitated a minimal level of spacing to allow equipment to move through the stands while still accomplishing the management objectives of the harvest and prescribed fire typically kills smaller trees. For these reasons, stand-level differences in structure were inherently a part of any treatment effects observed.

Overall, we found differences among snag treatments for several decay variables. Topped snags were more penetrable and had a higher proportion of loose bark remaining than the other treatments. Girdling produced snags that were generally much harder and less penetrable than even live trees. Snags generated by prescribed fire had levels of penetrability comparable to live trees, with any bark remaining being more adhered to the bole. There was also evidence of different levels of use by subcortical insects and birds among treatments. Treatment as a variable was, by itself, shown to be a significant predictor of the abundance of foraging excavations and presence of cavities. Snag diameter was also found to be an important predictor of cavity presence, arguably to a greater degree than treatment.

Some of the unique decay characteristics we observed among treatments have previously been documented in studies from other types of conifer forests. For instance, topped snags decayed faster than other snag treatments tested in a number of studies conducted in western forests of the United States (Bull and Partridge, 1986, Hallett et al., 2001, Lehmkuhl et al., 2003; Filip et al., 2004). High levels of retained loose bark on topped trees may retain moisture within the sapwood of snags. Topping itself also creates a flat, exposed surface that readily collects moisture, providing suitable conditions for fungi and microbes (Harmon et al., 1986). Topped snags were also used more heavily by insects, which could have further facilitated microbial colonization and decay (Harmon et al., 1986).

We found that girdled snags were generally harder than snags from the other treatments and had lower levels of insect activity and bird excavations. Past studies have found that mechanical girdling resulted in snags that decayed slower than other treatments (Bull and Partridge, 1986, Hallett et al., 2001, Parks et al., 1999, Shea et al., 2002). Girdled snags have also been found to break at faster rates than other snag creation treatments, such as topping (Hallett et al., 2001). Within the same stands studied herein, Corace et al. (2013) found that categorical rates of decay classes were influenced by the cause of death. In particular, a greater percentage of girdled trees developed more advanced classes of decay (associated with breaking) faster than other snag creation treatments. It is possible that girdling caused desiccation of the sapwood at the middle sections on the stems where bark had been reduced. Drying wood cells shrink as moisture is lost and there is generally a decrease in plasticity of the wood (Panshin and de Zeeuw, 1980). Thus, moisture loss midway up the bole on girdled snags may have contributed to snags breaking more readily.

We expected that more bird foraging activity would occur on snags with more insect use, but we did not find this to be true. Instead, we found that topped snags showed the greatest levels of subcortical insect use while snags generated by prescribed fire had the most foraging excavations, contrary to what one might expect if birds were specifically targeting foraging sites based solely on subcortical insect abundance. This suggests that birds were foraging based on additional cues. Because treatments were applied at different sites, each treatment encompassed environmental factors not measured in this study. These unknown variables may have played a role in foraging site selection and possibly influenced the use of snags by a species such as the black-backed woodpecker, a known post-fire specialist that shows a strong preference for recently burned forests (Nappi et al., 2010). Past work by Youngman and Gayk (2011) noted the irruptive nature and high population density of black-backed woodpeckers following fire in pine-dominated ecosystems of eastern Upper Michigan. It is possible that the environmental cue of a recent fire is the most important factor for locating preferred foraging habitat for this species. Given their known occurrence in the region, this species may have been responsible for a large proportion of the excavations observed in the prescribed fire treatment.

The model containing snag DBH performed best at predicting the presence of cavities on snags. This finding is consistent with other studies that have found larger snags to be preferred by primary cavity-nesters (Parks et al., 1999, Lehmkuhl et al., 2003, Farris and Zack, 2005). Most studies have generally shown that primary cavity-nesters preferentially target larger trees that have experienced a certain level of heart rot (Conner et al., 1976, Lehmkuhl et al., 2003, Nappi et al., 2003, Farris and Zack, 2005, Bagne et al., 2008). This should have made the topped snags preferable, being generally larger in diameter and potentially more easily penetrable. However, birds are likely balancing several factors beyond ease of excavation when creating a cavity. Blanc and Martin (2012) looked at decay profiles of cavity trees in aspen (*Populus*) forests and found that woodpeckers traded off ease of excavation with tree security, and often selected unhealthy live trees for nesting. Because topped snags were restricted in height to ~3 m, some primary cavity-nesters may have chosen not to use the snags we created (Table 1). Unfortunately, this shorter height was a limitation imposed by the logging equipment and future studies in this region might consider exploring topping snags through other means.

A wide range of forest wildlife use dead woody material throughout their life cycles. Our aim was not only to identify treatment-specific characteristics of snags that were preferred by primary cavity-nesters, but to also infer on the usefulness of snag treatments for other taxa (Table 7). In particular, loose, retained bark on snags may provide shelter for a number of wildlife taxa other than birds. Over the course of this research, we found two species of snakes (*Opheodrys vernalis, Storeria occipitomaculata*) and one tree frog (*Hyla versicolor*) beneath the loose bark at the base of topped snags. Also, although we did not observe any, some species of bats–including the threatened northern long-eared bat (*Myotis septentrionalis*) – are known to roost beneath exfoliating or loose bark (Foster and Kurta, 1999). Therefore, management aimed at benefitting such species might consider a treatment where bark is retained and is adhered more loosely to the snag (topping). Conversely, herpetofauna and small mammals benefit from dead material as cover on the forest floor (Maser et al., 1979, Bull, 2002). Individuals may therefore benefit more from a treatment that resulted in stem breakage soon after tree death and downed woody material that is sound (girdling).

**Table 7**
Potential wildlife implications associated with jack pine snags created using three methods (i.e., girdling, topping, and prescribed fire) based on major snag characteristics associated with each treatment type at Seney National Wildlife Refuge.

| Treatment | Major snag characteristic(s) | Implications for birds | Implications for mammals | Implications for herptofauna |
|---|---|---|---|---|
| Girdled | ● Low bark retention at site where girdling occurred<br>● Wood density is highest and wood is relatively harder<br>● Prone to breaking<br>● Lowest level of colonization by subcortical insects | Of all three treatments, this may be the one with the lowest snag value for cavity-nesting birds over periods of 9–13 years. The hardness of wood and lower insect use may preclude foraging by some birds, and we found few cavities present on sampled snags. Nonetheless, for perching species (e.g., raptors) the soundness of wood may be useful. | As a snag, they are unlikely to have high value for mammals relative to other treatments. Due to the soundness of the material, however, this treatment may yield long-lasting, coarse woody material benefiting small mammals as cover over time. | As a snag, they are unlikely to have much value relative to other treatments. Due to the soundness of the material, however, this treatment may yield long-lasting, coarse woody material benefiting herptofauna as cover over time. |
| Topped | ● High bark retention<br>● Greater proportions of loose bark<br>● Wood is relatively softer, less dense<br>● Most heavily colonized by subcortical insects | Use by insects is relatively high. Decay and wood softness resulting from this treatment may provide a substrate that is easily excavated for weaker cavity-nesters, such as nuthatches and chickadees. However, the height of this specific treatment may preclude cavity excavation by some species. Loose bark can be used as resting cover for some small birds. | Possibly high value for bats due to high bark retention and bark looseness. Combined with high levels of insect use, this treatment could provide feeding sites and cover for rodents as well. | Possibly high use by herptofauna due to high bark retention and bark looseness. Two snake species and one tree frog were observed beneath the bark of topped snags during the course of this study. |
| Prescribed Fire | ● Low bark retention<br>● Greater adherence of remaining bark<br>● Wood hardness is similar to that of live trees<br>● 2nd most colonized by subcortical insects | As other studies show and this study further supports, this treatment is likely preferred (or necessary) for many primary cavity-nesters. | In terms of amount of bark present, possibly lower use by bats and mammals in short-term. However, over time the remaining bark may become less adhered and provides cover for bats and small mammals. | In terms of amount of bark present, possibly lower use by herptofauna in short-term. However, over time the remaining bark may become less adhered and provide cover for herpetofauna. |

## 5. Limitations

There are several limitations to consider when interpreting our results. First, due to the opportunistic design of the study, each treatment was confined to a specific area of the landscape and not replicated at multiple locations. Thus, site effects may have contributed to the observed treatment effects. However, site characteristics were relatively uniform across treatments with forest soil type, structure, composition, topography, and site history all similar (see Methods). Second, each treatment was implemented in a different year, so we were not able to account for time since treatment as a variable. However, if most of the foraging and insect activity occurred within three years of tree death as shown in previous studies (Farris et al., 2002, Farris and Zack, 2005), this should have had little effect on the results of our foraging model. There were also treatment effects resulting from the manner in which the treatments were implemented. In particular, girdling resulted in a lack of insect or bird activity on the middle, debarked section of the bole. This also likely affected associated decay processes, regardless of time since treatment. Lastly, this study focused primarily on jack pine snags. Snags in mixed-pine ecosystems of the Great Lakes region exhibit species-specific decay rates (Corace et al., 2013), so our results may not hold true for other tree species.

## 6. Conclusions

This study contributes region-specific knowledge regarding wildlife use of managed snags within Great Lakes mixed-pine forests. Biological legacies, such as snags, play an important role in ecosystem function. Great Lakes forest mangers seeking to conserve or restore mixed-pine forest ecosystems and manage them for the benefit of multiple taxa may desire to incorporate these features in their forest treatments. One potential application of this knowledge is in northern Lower Michigan jack pine stands managed for the Kirtland's warbler. Current management practices to promote Kirtland's warbler breeding habitat commonly consist of harvesting and replanting jack pine in an opposing wave pattern meant to emulate conditions that arise from stand-replacing fires that were historically more common (MDNR et al., 2015). However, many patterns that result from prescribed fire or wildfire in jack pine forests are not present in jack pine plantations for Kirtland's warbler. Plantations differ from stands that originate following fire in overall stem density and patchiness (Kashian et al., 2017), as well as the amount, spatial configuration, and longevity of biological legacies (Spaulding and Rothstein, 2009, Corace et al., 2010, Kashian et al., 2012). Therefore, there may be opportunities for managers to consider incorporating snag treatments as shown here into harvesting done in mature stands before jack pine seedlings are planted.

It is important to consider that different methods of creating forest structures, such as snags, result in variable patterns of subsequent decay. Consequently, use by target wildlife species will likely vary depending on the treatment chosen and wildlife community present. Furthermore, some specialist wildlife species likely have other ways of identifying quality foraging and breeding habitat beyond the presence of dead trees. Snags provide important habitat features for mammals, herpetofauna, insects, and birds. Knowledge of the decay characteristics that result from these snag creation treatments and how they may affect various taxa can be useful for managers when considering snag treatment options that align with their management objectives.

## Acknowledgments

We thank Sarah Rademacher, Lyndsay Morrison, and Tayelor Gosselin for their help with data collection. Laurie Tansy and other SNWR staff are thanked for logistical support. We also thank two anonymous reviewers whose suggestions greatly improved this work. Funding was provided by The Ohio State University, Seney National Wildlife Refuge, and the Seney Natural History Association. The findings and conclusions are those of the authors and do not necessarily represent the views of the U.S. Fish and Wildlife Service.

## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2017.10.013.

## References

Albert, D.A. 1995. Regional Landscape Ecosystems of Michigan, Minnesota, and Wisconsin: A Working Map and Classification. USDA Forest Service Gen. Tech. Rep. NC-178.

Angers, V.A., Bergeron, Y., Drapeau, P., 2012. Morphological attributes and snag classification of four North American boreal tree species: relationships with time since death and wood density. For. Ecol. Manage. 263, 138–147. http://dx.doi.org/10.1016/j.foreco.2011.09.004.

Arnett, E.B., Kroll, A.J., Duke, S.D., 2010. Avian foraging and nesting use of created snags in intensively-managed forests of western Oregon, USA. For. Ecol. Manage. 260 (10), 1773–1779. http://dx.doi.org/10.1016/j.foreco.2010.08.021.

Bagne, K.E., Purcell, K.L., Rotenberry, J.T., 2008. Prescribed fire, snag population dynamics, and avian nest site selection. For. Ecol. Manage. 255 (1), 99–105. http://dx.doi.org/10.1016/j.foreco.2007.08.024.

Bergeron, Y., Richard, P.J.H., Carcaillet, C., Gauthier, S., Flannigan, M., Prairie, Y., 1998. Variability in fire frequency and forest composition in Canada's southeastern boreal forest: a challenge for sustainable forest management. Conserv. Ecol. 2 (2).

Blanc, L.A., Martin, K., 2012. Identifying suitable woodpecker nest trees using decay selection profiles in trembling aspen (*Populus tremuloides*). For. Ecol. Manage. 286, 192–202.

Bliss, C.I., Fisher, R.A., 1953. Fitting the negative binomial distribution to biological data. Biometrics 9 (2), 176–200. http://dx.doi.org/10.2307/3001850.

Boddy, L., 2001. Fungal community ecology and wood decomposition processes in angiosperms: from standing tree to complete decay of coarse woody debris. Ecol. Bull. 49, 43–56. http://www.jstor.org/stable/20113263.

Boulanger, Y., Sirois, L., 2007. Postfire succession of saproxylic arthropods, with emphasis on coleoptera, in the north boreal forest of Quebec. Environ. Entomol. 36 (1), 128–141. http://dx.doi.org/10.1603/0046-225X-36.1.128.

Brandeis, T.J., Newton, M., Filip, G.M., Cole, E.C., 2002. Cavity-nester habitat development in artificially made douglas-fir snags. J. Wildl. Manage. 66 (3), 625–633. http://dx.doi.org/10.2307/3803129.

Browse Species. Birds of North America Online. The Cornell Lab of Ornithology < birdsna.org/Species-Account/bna/species > (Accessed on 11 October 2017).

Bull, E.L., 2002. The value of coarse woody debris to vertebrates in the Pacific Northwest. USDA Forest Service Gen. Tech. Rep. PSW-GTR-181.

Bull, E.L., Partridge, A.D., 1986. Methods of killing trees for use by cavity nesters. Wildl. Soc. Bull. 14 (2), 142–146. http://www.jstor.org/stable/3782061.

Burger, T.L., Kotar, J., 2003. A Guide to Forest Communities and Habitat Types of Michigan. University of Wisconsin Press, Madison, WI.

Burnham, K.P., Anderson, D.R., 2002. Information and Likelihood Theory: A Basis for Model Selection and Inference. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, second ed. New York, Springer.

Byers, J.A., 1995. Host-Tree Chemistry Affecting Colonization in Bark Beetles. In: Chemical Ecology of Insects, vol. 2. Springer, pp. 154–213.

Chambers, C.L., Carrigan, T., Sabin, T.E., Tappeiner, J., McComb, W.C., 1997. Use of artificially created douglas-fir snags by cavity-nesting birds. Western J. Appl. For. 12 (3), 93–97.

Chartier, A.T., Baldy, J.J., Brenneman, J.M., 2011. The Second Michigan Breeding Bird Atlas, 2002–2008. Kalamazoo Nature Center, Kalamazoo, MI.

Conner, R.N., Miller Jr, O.K., Adkisson, C.S., 1976. Woodpecker dependence on trees infected by fungal heart rots. Wilson Bull. 575–581. http://www.jstor.org/stable/4160827.

Cooper, C., Bonter, D., 2008. Artificial nest site preferences of black-capped chickadees. J. Field Ornithol. 79 (2), 193–197.

Corace III, R.G., Shartell, L.M., Goebel, P.C., Kashian, D.M., Drobyshev, I., Hix, D.M., 2014. Bird communities of reference and altered mixed-pine forests: implications for restoring fire-dependent ecosystems. For. Ecol. Manage. 318, 183–193.

Corace III, R.G., Stout, A.T., Goebel, P.C., Hix, D.M., 2013. Snag benchmarks and treatment options for mixed-pine forest restoration in eastern Upper Michigan. Restor. Ecol. 21 (5), 608–616. http://dx.doi.org/10.1111/j.1526- 100X.2012.00929.x.

Corace III, R.G., Goebel, P.C., Hix, D.M., Casselman, T., Seefelt, N.E., 2009. Ecological forestry at National Wildlife Refuges: experiences from Seney National Wildlife Refuge and Kirtland's Warbler Wildlife Management Area, USA. For. Chron. 85 (5), 695–701. http://dx.doi.org/10.5558/tfc85695-5.

Corace III, R.G., Seefelt, N.E., Goebel, P.C., Shaw, H.L., 2010. Snag longevity and decay class development in a recent jack pine clearcut in Michigan. Northern J. Appl. For. 27 (4), 125–131.

Drever, C.R., Peterson, G., Messier, C., Bergeron, Y., Flannigan, M., 2006. Can forest management based on natural disturbances maintain ecological resilience? Can. J. For. Res. 36 (9), 2285–2299. http://dx.doi.org/10.1139/x06-132.

Drobyshev, I., 2014. Understanding the Importance of Spatially-Explicit Metrics of Natural Disturbance Regimes in Restoration of Mixed-Pine Forests. LSFSC Research Brief for Resouce Managers RB-14-4.

Drobyshev, I., Goebel, P.C., Hix, D.M., Corace III, R.G., Semko-Duncan, M.E., 2008a. Interactions among forest composition, structure, fuel loadings and fire history: a case study of red pine-dominated forests of Seney National Wildlife Refuge, Upper Michigan. For. Ecol. Manage. 256 (10), 1723–1733. http://dx.doi.org/10.1016/j.foreco.2008.05.017.

Drobyshev, I., Goebel, P.C., Hix, D.M., Corace III, R.G., Semko-Duncan, M.E., 2008b. Pre- and post-European settlement fire history of red pine dominated forest ecosystems of Seney National Wildlife Refuge, Upper Michigan. Can. J. For. Res. 38 (9), 2497–2514. http://dx.doi.org/10.1139/X08-082.

Dudley, N., Vallauri, D., 2005. Restoration of Deadwood as a Critical Microhabitat in Forest Landscapes. In: Forest Restoration in Landscapes. Springer, New York, pp. 203–207. http://dx.doi.org/10.1007/0-387-29112-1_29.

Farris, K.L., Garton, E.O., Heglund, P.J., Zack, S., Shea, P.J., 2002. Woodpecker Foraging and the Successional Decay of Ponderosa Pine. USDA Forest Service Gen. Tech. Rep. PSW-GTR-181.

Farris, K.L., Huss, M.J., Zack, S., 2004. The role of foraging woodpeckers in the decomposition of ponderosa pine snags. The Condor 106 (1), 50–59. http://dx.doi.org/10.1650/7484.

Farris, K.L., Zack, S., 2005. Woodpecker-Snag Interactions: An Overview of Current Knowledge in Ponderosa Pine Systems. pp. 18–21. http://www.treesearch.fs.fed.us/pubs/27268.

Filip, G.M., Parks, C.G., Baker, F.A., Daniels, S.E., 2004. Technical note—artificial inoculation of decay fungi into Douglas-Fir with rifle or shotgun to produce wildlife trees in western Oregon. Western Journal of Applied Forestry 19 (3), 211–215.

Flower, C.E., Knight, K.S., Rebbeck, J., Gonzalez-Meler, M.A., 2013. The relationship between the emerald ash borer (*Agrilus planipennis*) and ash (*Fraxinus* spp.) tree decline: using visual canopy condition assessments and leaf isotope measurements to assess pest damage. For. Ecol. Manage. 303 (September), 143–147. http://dx.doi.org/10.1016/j.foreco.2013.04.017.

Foster, R.W., Kurta, A., 1999. Roosting ecology of the northern bat (*Myotis septentrionalis*) and comparisons with the endangered Indiana bat (*Myotis sodalis*). J. Mammal. 80 (2), 659–672. http://dx.doi.org/10.2307/1383310.

Franklin, J., 1988. Structural and functional diversity in temperate forests. Biodiversity 166–175.

Franklin, J.F., Forman, R.T.T., 1987. Creating landscape patterns by forest cutting: ecological consequences and principles. Landscape Ecol. 1 (1), 5–18. http://dx.doi.org/10.1007/BF02275261.

Franklin, J.F., Spies, T.A., Van Pelt, R., Carey, A.B., Thornburgh, D.A., Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K., Chen, J., 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using douglas-fir forests as an example. For. Ecol. Manage. 155 (1–3), 399–423. http://dx.doi.org/10.1016/S0378-1127(01)00575-8.

Gorman, G., 2015. Foraging signs and cavities of some European woodpeckers (Picidae): identifying the clues that lead to establishing the presence of species. Denisia 36, 87–97.

Hallett, J.G., Lopez, T., O'Connell, M.A., Borysewicz, M.A., 2001. Decay dynamics and avian use of artificially created snags. Northwest Sci. 75 (4), 378–386. http://hdl.handle.net/2376/971.

Harmon, M.E., 2001. Moving towards a new paradigm for woody detritus management. Ecol. Bull. 269–278. http://www.jstor.org/stable/20113283.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., 1986. Ecology of coarse woody debris in temperate ecosystems. Adv. Ecol. Res. 15, 133–302. http://dx.doi.org/10.1016/S0065-2504(08)60121-X.

Holloway, G.L., Malcolm, J.R., 2007. Nest-tree use by northern and southern flying squirrels in central Ontario. J. Mammal. 88 (1), 226–233. http://dx.doi.org/10.1644/05- MAMM-A-368R2.1.

Jackson, J.A., 1976. A comparison of some aspects of the breeding ecology of red-headed and red-bellied woodpeckers in Kansas. The Condor 78 (1), 67–76. http://dx.doi.org/10.2307/1366917.

Johnson, K.G., Pelton, M.R., 1981. Selection and availability of dens for black bears in Tennessee. J. Wildl. Manage. 45 (1), 111–119. http://dx.doi.org/10.2307/3807879.

Jonsell, M., Weslien, J., 2003. Felled or standing retained wood—it makes a difference for saproxylic beetles. For. Ecol. Manage. 175 (1–3), 425–435. http://dx.doi.org/10.1016/S0378-1127(02)00143-3.

Jonsson, B.G., Kruys, N., Ranius, T., 2005. Ecology of species living on dead wood– lessons for dead wood management. Silva Fennica 39 (2), 289–309.

Kashian, D.M., Corace III, R.G., Shartell, L.M., Donner, D.M., Huber, P.W., 2012. Variability and persistence of post-fire biological legacies in jack pine-dominated ecosystems of northern Lower Michigan. For. Ecol. Manage. 263, 148–158. http://dx.doi.org/10.1016/j.foreco.2011.09.019.

Kashian, D.M., Sosin, J.R., Huber, P.W., Tucker, M.M., Dombrowski, J., 2017. A neutral modeling approach for designing spatially heterogeneous jack pine plantations in northern Lower Michigan, USA. Landscape Ecol. 32 (6), 1117–1131. http://dx.doi.org/10.1007/s10980-017-0514-y.

Lehmkuhl, J.F., Everett, R.L., Schellhaas, R., Ohlson, P., Keenum, D., Riesterer, H., Spurbeck, D., 2003. Cavities in snags along a wildfire chronosequence in eastern Washington. The J. Wildl. Manage. 67 (1), 219–228. http://dx.doi.org/10.2307/3803077.

Lindenmayer, D.B., Franklin, J.F., 2002. Conserving Forest Biodiversity: A Comprehensive Multiscaled Approach. Island Press.

Lindenmayer, D.B., Noss, R.F., 2006. Salvage logging, ecosystem processes, and biodiversity conservation. Conserv. Biol. 20 (4), 949–958. http://dx.doi.org/10.1111/j.1523-1739.2006.00497.x.

Lonsdale, D., Pautasso, M., Holdenrieder, O., 2008. Wood-decaying fungi in the forest: conservation needs and management options. Eur. J. Forest Res. 127 (1), 1–22. http://dx.doi.org/10.1007/s10342-007-0182-6.

Losey, E.B., 2003. Seney National Wildlife Refuge: Its Story. Lake Superior Press, Marquette, MI.

Maser, C., Anderson, R.G., Cromack Jr, K., Williams, J.T., Martin, R.E., 1979. Dead and down Woody Material. Wildlife Habitats in Managed Forests: The Blue Mountains of Oregon and Washington. Agriculture Handbook No. 553. pp. 78–95.

Michigan Department of Natural Resources (MDNR), U.S. Fish and Wildlife Service, and U.S. Forest Service. 2015. Kirtland's Warbler Breeding Range Conservation Plan. Lansing, MI.

Midwestern Regional Climate Center (MRCC). 2017. Midwest Climate: Climate Summaries. Illinois State Water Survey, Prairie Research Institute, University of Illinois at Urbana-Champaign. http://mrcc.isws.illinois.edu/mw_climate/climateSummaries/climSumm.jsp accessed on: 09/06/2017.

Nappi, A., Drapeau, P., Giroux, J., Savard, J.L., Moore, F., 2003. Snag use by foraging black-backed woodpeckers (*Picoides arcticus*) in a recently burned eastern boreal forest. The Auk 120 (2), 505–511. http://dx.doi.org/10.1642/0004-8038.

Nappi, A., Drapeau, P., Saint-Germain, M., Angers, V.A., 2010. Effect of fire severity on long-term occupancy of burned boreal conifer forests by saproxylic insects and wood-foraging birds. Int. J. Wildl. Fire 19 (4), 500–511. http://dx.doi.org/10.1071/WF08109.

Nyamai, P.A., 2013. Factors Affecting Regeneration-Layer Dynamics in Mixed-Pine Forest Ecosystems of Eastern Upper Michigan and Implications for Forest Ecosystem Restoration. Ph.D. Dissertation. The Ohio State University, Columbus, OH.

Nyamai, P.A., Goebel, P.C., Hix, D.M., Corace III, R.G., Drobyshev, I., 2014. Fire history, fuels, and overstory effects on the regeneration-layer dynamics of mixed-pine forest ecosystems of eastern Upper Michigan, USA. For. Ecol. Manage. 322, 37–47.

Panshin, A.J., de Zeeuw, C., 1980. Textbook of Wood Technology. McGraw-Hill Book Company, New York, NY.

Parks, C.G., Conklin, D.A., Bednar, L., Maffei, H., 1999. Woodpecker Use and Fall Rates of Snags Created by Killing Ponderosa Pine Infected with Dwarf Mistletoe. http://www.treesearch.fs.fed.us/pubs/2911.

Perry, D.A., 1998. The scientific basis of forestry. Annu. Rev. Ecol. Syst. 29 (1), 435–466. http://dx.doi.org/10.1146/annurev.ecolsys.29.1.435.

Petit, D.R., Petit, K.E., Grubb, T.C., Reichhardt, L.J., 1985. Habitat and snag selection by woodpeckers in a clear-cut: an analysis using artificial snags. The Wilson Bulletin 97 (4), 525–533. http://www.jstor.org/stable/4162147.

R Core Team 2013. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. Vienna, Austria. http://www.R-project.org/.

Saint-Germain, M., Drapeau, P., Hébert, C., 2004. Landscape-scale habitat selection patterns of *Monochamus scutellatus* (Coleoptera: Cerambycidae) in a recently burned black spruce forest. Environ. Entomol. 33 (6), 1703–1710. http://dx.doi.org/10.1603/0046- 225X-33.6.1703.

Saint-Germain, M., Drapeau, P., Buddle, C.M., 2007. Host-use patterns of saproxylic phloeophagous and xylophagous coleoptera adults and larvae along the decay gradient in standing dead black spruce and aspen. Ecography 30 (6), 737–748. http://dx.doi.org/10.1111/j.2007.0906-7590.05080.x.

Schulte, L.A., Mladenoff, D.J., Crow, T.R., Merrick, L.C., Cleland, D.T., 2007. Homogenization of northern US Great Lakes forests due to land use. LandscapeEcology 22 (7), 1089–1103. http://dx.doi.org/10.1007/s10980-007-9095-5.

Shea, P.J., Laudenslayer Jr, W.F., Ferrell, G., Borys, R., 2002. Girdled versus Bark Beetle-Created Ponderosa Pine Snags: Utilization by Cavity-Dependent Species and Differences in Decay Rate and Insect Diversity. USDA Forest Service Gen. Tech. Rep. PSW-GTR-181.pp. 145–153.

Spaulding, S.E., Rothstein, D.E., 2009. How well does Kirtland's warbler management emulate the effects of natural disturbance on stand structure in Michigan jack pine forests? For. Ecol. Manage. 258 (11), 2609–2618. http://dx.doi.org/10.1016/j.foreco.2009.09.020.

Thomas, J., 1979. Wildlife Habitats in Managed Forests–the Blue Mountains of Oregon and Washington. Aspen Bibliography Agriculture Handbook 553 (January). http://digitalcommons.usu.edu/aspen_bib/4604.

Torsten, H., Bretz, F., Westfall, P., 2008. Simultaneous inference in general parametric models. Biometr. J. 50 (3), 346–363.

Tucker, M.M., Corace III, R.G., Cleland, D.T., Kashian, D.M., 2016. Long-term effects of managing for an endangered songbird on the heterogeneity of a fire-prone landscape. Landscape Ecol. 1–14. http://dx.doi.org/10.1007/s10980-016-0413-7.

U.S. Fish and Wildlife Service (USFWS), 2009. Seney National Wildlife Refuge Comprehensive Conservation Plan. Regional Office, Fort Snelling, MN.

Venables, W.N., Ripley, B.D., 2002. Modern Applied Statistics with S, Fourth ed. Springer, New York.

Wood, D.L., 1982. The role of pheromones, kairomones, and allomones in the host selection and colonization behavior of bark beetles. Annu. Rev. Entomol. 27 (1), 411–446. http://dx.doi.org/10.1146/annurev.en.27.010182.002211.

Youngman, J.A., Gayk, Z.G., 2011. High density nesting of black-backed woodpeckers (*Picoides arcticus*) in a post-fire Great Lakes jack pine forest. Wilson J. Ornithol. 123 (2), 381–386. http://www.jstor.org/stable/23033407.